High-tide habitat choice

Rogers, Danny I.; Battley, Phil F.; Piersma, Theunis; Van Gils, Jan A.; Rogers, Ken G.

Published in:
Animal Behavior

DOI:
10.1016/j.anbehav.2005.10.029

Publication date:
2006

ANIMAL BEHAVIOUR, 2006, 72, 563–575
doi:10.1016/j.anbehav.2005.10.029

High-tide habitat choice: insights from modelling roost selection by shorebirds around a tropical bay

DANNY I. ROGERS*, PHIL F. BATTLEY†, THEUNIS PIERSMA‡§, JAN A. VAN GILS‡§ & KEN G. ROGERS
*Johnstone Centre, Charles Sturt University, Australia
†Australian School of Environmental Studies, Griffith University, Australia
‡Department of Marine Ecology and Evolution, Royal Netherlands Institute for Sea Research, The Netherlands
§Centre for Ecological and Evolutionary Studies, University of Groningen, The Netherlands

*(Received 23 June 2004; initial acceptance 13 October 2004;
final acceptance 26 October 2005; published online 12 July 2006; MS. number: 8174R)*

High tides force shorebirds from intertidal feeding areas to sites known as roosts. We investigated the roost selection of great knots, *Calidris tenuirostris*, and red knots, *Calidris canutus*, on a tropical coastline in northwestern Australia, assessing several roost attributes and recording the frequency of use of each site through automatic radiotelemetry. To model roost choice we used two approaches: (1) conditional logistic regression models that assumed roost selection to be a trade-off based on a probabilistic assessment of several environmental characteristics; and (2) bounds-based models that assumed that birds selected the nearest roost site to their feeding grounds, provided that threshold values for certain environmental characteristics were met. Bounds-based models were more effective, and we suggest that they offer a closer approach to real roost choice mechanisms. By day, roost choice was affected by distance from the feeding area and microclimate; birds selected nearby roosts where they could stand on cool, wet substrates. Different roost selection criteria were used at night when birds chose safer, but more distant, roosts. Models that assumed that roost choice was influenced by recent experience of roost sites performed better than models that assumed constant assessment of roost quality. This effect was significant only at night, suggesting that memory was used more when information on roost quality was limited. Evidence that roost availability may influence selection of foraging areas is also presented. Our results suggest that shorebirds select roosts by using simple mechanisms, making roost choice models a potentially valuable tool in conservation planning.

The majority of animals have well-defined daily routines: they optimize the use of places and times to eat and sleep (Daan 1981). However, in studies of the distribution of animals, the usual focus is on foraging in relation to food resources. Animals have to manage several currencies other than food intake, and the need for safety during both feeding and nonfeeding periods is important. In this study we focus on roost site choice in daylight and in darkness in animals (shorebirds) for which the feeding grounds become inaccessible twice a day.

Many coastal shorebirds are specialized to feed on intertidal flats which can be used only when the tide is low. At high tide they are forced to alternative sites, usually known as roosts. Shorebirds spend much time roosting, and individual roosts may hold thousands of birds at one time. High-tide roosts tend to be small areas on coastlines near to but just above the tide line, a combination of characteristics that makes them vulnerable to human development or disturbance (e.g. Mitchell et al. 1988). Active conservation measures are sometimes therefore needed to protect or even to create roost sites (e.g. Burton et al. 1996; Rehfisch et al. 1996, 2003). However, little is known about how shorebirds decide where to roost (Myers 1984; Luís et al. 2001; Rogers 2003).

Two ultimate principles are likely to underlie the choice of high-tide roost sites. First, shorebirds should roost

Correspondence and present address: D. I. Rogers, 340 Nink's Road, St Andrews, Victoria 3761, Australia (email: drogers@melbpc.org.au). P. F. Battley is now at the School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand. T. Piersma is at the Royal Netherlands Institute for Sea Research (NIOZ) and the Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 45, 9750 AA Haren, The Netherlands. J. A. van Gils is now at the Netherlands Institute of Ecology (NIOO-KNAW), Centre for Limnology, Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands. K. G. Rogers is at 340 Nink's Road, St Andrews, Victoria 3761, Australia.

0003–3472/06/$30.00/0

where the risk of predation is low. Second, they should minimize energy expenditure over the high-tide period. This may be especially important to migratory species, as their life cycle includes tightly scheduled periods of rapid gain in mass when their energy intake is much greater than that simply needed for maintenance (Lindström 1991; Piersma et al. 1994, 2005; Piersma & Baker 2000). Other things being equal, high-tide energy expenditure will be lowest if high-tide roosts are close to the low-tide feeding areas, so little energy needs to be spent 'commuting' (Piersma et al. 1993). There may, however, be situations in which a more distant roost is a more economical option, because it has either (1) low disturbance rates, so little energy needs to be spent avoiding potential predators (Davidson & Rothwell 1993) or (2) a relatively mild microclimate, in which energetic costs of thermoregulation are low (Wiersma & Piersma 1994). There may therefore be trade-offs between travel costs and energy expenditure at the selected roost site. Roost choices made by shorebirds may also involve trade-offs between the risks of predation and high energy expenditure, for example, in situations where a roost that appears suitable from energetic considerations happens to have a high risk of raptor predation (cf. Cresswell 1994).

We used a model-building approach to investigate the roost choice of two large species of migratory sandpiper: great knot, *Calidris tenuirostris*, and red knot, *Calidris canutus*. At our study site in Roebuck Bay, a tropical nonbreeding area on the northwestern Australian coast, both species feed exclusively on intertidal flats. The bay is well suited for studies of roost choice, as it has several different habitats where the two knot species may congregate at high tide to roost in large, mixed-species flocks (Rogers & Taylor 2001; Rogers et al. 2003). The environmental characteristics of these roost sites vary with the large local tides. We modelled roost selection at different times and tidal conditions, comparing the predicted usage of roost sites with that observed in the course of an intensive radiotelemetric study. The models were used to test or investigate the following hypotheses.

(1) Roost selection criteria differ by day and night. By day, shorebirds often evade diurnal birds of prey through early detection and alarm flights (e.g. Whitfield 2003). In darkness, these escape ploys are likely to be difficult to perform, and shorebirds are in any case likely to be at risk from different predators, such as owls or terrestrial mammals, that could catch a shorebird only after a close approach by stealth (Sitters et al. 2001; Rogers 2003). At night we would therefore expect shorebirds to be more intolerant of roosts that offer potential cover for hunting predators.

(2) In tropical or other warm regions the need to stay cool influences roost choice. The lifestyle of migratory shorebirds is likely to expose them to the risk of heat stress. They live in open habitats exposed to direct solar radiation. In coastal birds without free access to fresh water, control of body temperature through cutaneous evaporative water loss is likely to be costly (Tieleman & Williams 1999). The extent to which they can reduce metabolic heat production is limited by seasonal changes in lean mass (associated with migratory preparation) which in turn influences the basal metabolic rate (Piersma et al. 1996). Shorebirds use heat avoidance behaviour such as ptiloerection (Battley et al. 2003), but the risk of heat stress may still influence their habitat choice.

(3) Shorebirds are not ideal and free when selecting roosts. Great and red knots are capable of direct flights of several thousand kilometres during migration (Battley et al. 2000), and the distances between feeding and roosting sites may seem negligible by comparison. If this flight is 'free' (i.e. effectively without time and energy costs) we would not expect the distance between feeding and roost sites to influence the success of roost choice models. Ideal birds would have complete knowledge of the attributes of all potential roost sites. If birds are not ideal, we would expect models that do not assume complete knowledge to be at least as effective at predicting roost choice as models that assume omniscience. We would also expect that birds would use experience as a source of information on roost quality, therefore preferring sites found adequate on the previous high tide, and this preference should be more marked in darkness, when shorebirds presumably find it harder to use distant views of a roost site to assess its quality. Finally, if roost selection is influenced by memory, the choice of foraging sites might be influenced by their proximity to the roosts that birds intend to use on the next high tide.

METHODS

Habitat Classification

Roebuck Bay (ca. 18°S, 122°E) is in the monsoonal tropics, on the coast of northwestern Australia. It is an internationally important nonbreeding area for migratory shorebirds, with nonbreeding populations of the study species exceeding 27 600 great knots and 2000 red knots (unpublished data). The bay has extensive intertidal flats where great and red knots feed (Rogers 1999; Rogers et al. 2003). The tide cycles are semidiurnal, usually with one high tide in the middle of each day and one high tide in the middle of each night. During neap series (ca. 20% of tides), high tides can occur within 2 h of dawn and dusk. Tidal range varies from only about 1 m on neaps to 8–10 m on spring tides (Pepping et al. 1999; Fig. 1). Much of the bay is fringed by dense mangroves, which are not used by roosting shorebirds. The key roost sites (Fig. 1) are all thought to have been located (Rogers & Taylor 2001), either by local birdwatchers or through directed searches (e.g. Collins et al. 2001). Another roost site, Kidneybean Claypan (Rogers et al. 2001) was too deeply flooded by local rainfall to be used by shorebirds during the study period from February to April 2000. It is not considered further in this paper.

Characteristics of roost sites were influenced by tide levels. The position of high and low water marks could be predicted accurately with tide timetables (National Tidal Facility, Flinder's University of South Australia); tidal ranges in Roebuck Bay are so large that they are relatively unaffected by changes in air pressure and winds. Neap high tides (<6 m) just covered the intertidal flats, with the

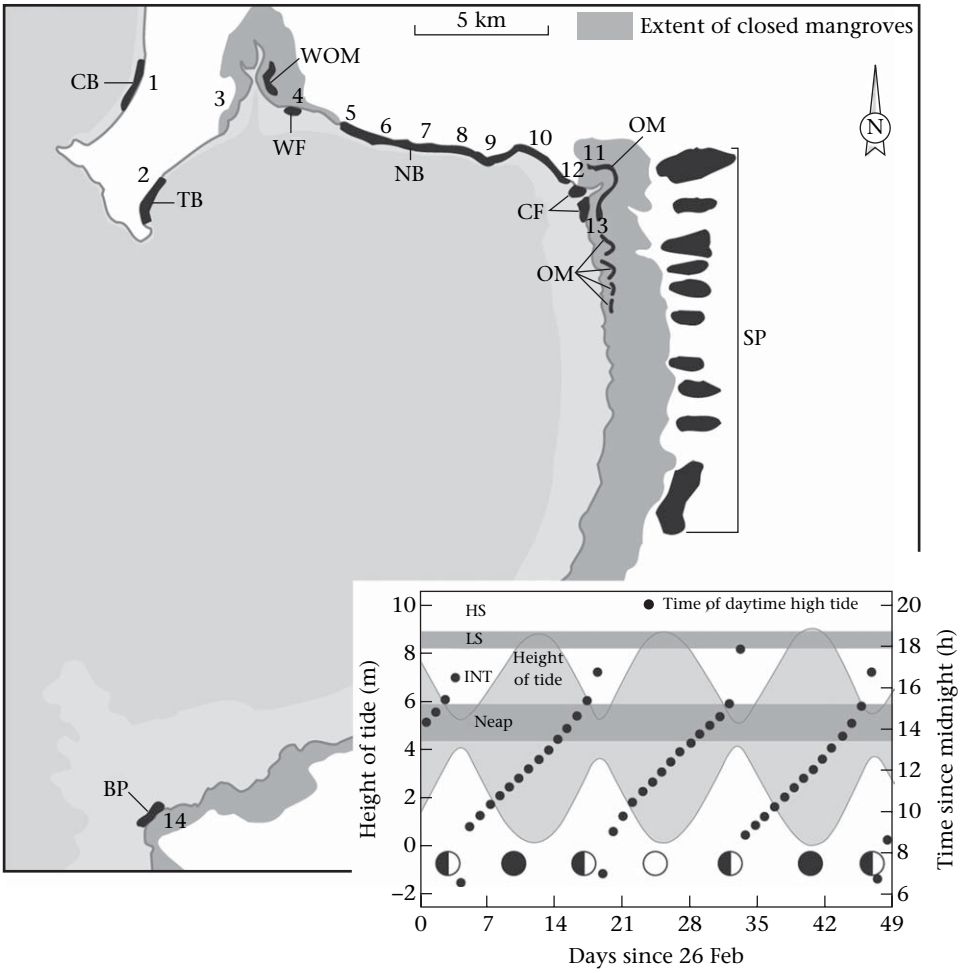

Figure 1. Map of the Roebuck Bay study site, adapted from aerial photographs. Numbers denote automatic radiotracking stations. The roosting habitats shown are CB (Cable Beach): white sand beach backed by unvegetated white dunes; CF (Crab Creek Flats): raised mudflats at the mouth of Crab Creek; WF (Western Flats): smaller raised mudflats, closer to tall cover; NB (Northern Beaches): red sand beaches backed by low laterite cliffs or vegetated dunes; some rocky points also occasionally used as roosts; TB (Town Beach): broader sandy beach backed by vegetated dunes; OM (Open Mangroves): clearings (ca. 100 m in diameter) in the Crab Creek mangrove forest; WOM (Western Open Mangroves): clearings in the Dampier Creek mangrove forest; SP (Salt pans): large unvegetated claypans, surrounded by saltmarsh; BP: white beaches and sandbar at Bush Point. Inset shows amplitude of tides in Roebuck Bay (plotted against the left *Y* axis) throughout the study period, 26 February to 15 April. The times of the peak daytime high tides are plotted against the right *Y* axis. Grey shading is used to depict high tides classified as low springs (LS: 8.3–8.95 m) and Neaps (>6.0 m); intermediate (INT) tides and high spring (HS) tides are also shown. Lunar phases are shown at the bottom of the graph.

exception of two areas of raised mud near creek mouths (CF and WF in Fig. 1). Intermediate high tides (6.0–8.2 m) reached on to the bases of the northern beaches and into the seaward parts of the mangroves. Low spring tides (8.3–8.95 m) reached higher on the northern beaches and further into the mangroves, partially covering roost sites in natural clearings (OM in Fig. 1). These clearings were deeply submerged on high spring tides (≥9 m), which flowed through the mangroves into the salt pans beyond (SP in Fig. 1). Clearings in the Western Open Mangroves (WOM in Fig. 1) were slightly higher than those in the eastern bay, and were not completely submerged by high spring tides. Spring tides exceeding 9 m occurred only by day during the study period.

We used four variables to describe roosts: (1) climate and (2) distance from feeding to roosting site were presumed to be related to the energetic costs of roosts; (3) background colour and (4) distance from tall cover were presumed to be related to predation risk. We measured distance (km) from feeding grounds to roosting sites directly. The remaining variables could not be measured continuously during the study because some of the more remote roosts could be visited only occasionally. Accordingly, we assigned simple ordinal values for these variables to each roost on each high tide (Table 1), using quantitative data as a guide.

We paced out distance to tall cover (m) from roosts to the nearest dunes, cliffs or vegetation taller than 1 m; we saw several species of raptor using such landforms or vegetation to conceal a high-speed attack on shorebird roosts. At some sites the distance from roosts to tall cover varied according to tide level, so we took measurements on

Table 1. Categorical indexes of roost quality at Roebuck Bay roosts

	Daytime high tides				Night-time high tides		
Roost	Neap	Intermediate	Low spring	High spring	Neap	Intermediate	Low spring
NB	122	132	142	242	122	132	142
CF	111	451	451	451	111	451	451
CB	111	121	131	131	111	121	131
BP	111	111	121	121	111	111	121
WF	142	452	452	452	142	452	452
WOM	333	343	243	133	143	143	143
OM	333	333	133	243	143	143	143
SP	311	311	111	111	111	111	111
TB	122	132	132	132	122	132	132

Indexes are presented as three-digit numbers representing, in sequence, the category scores for microclimate, distance from tall cover and background colour. The higher the category score, the less suitable the index of roost quality. Climate scores used at WOM, OM and SP were corrected in some cases to account for local rainfall. High tides were categorized as neap (<6 m), intermediate (6.0–8.2 m), low spring (8.3–8.95 m) or high spring (≥9 m).

a range of tide heights. Distance from tall cover was categorized as (1) >200 m, (2) 60–199 m, (3) 10–59 m, (4) 1–9 m; and (5) <1 m.

Background colour of the tall cover within 200 m of roosts was classified as mostly pale (category 1: no nearby tall cover, or unvegetated white sand dunes on one side of the roost), mostly dark (category 3: surrounded by dark green mangroves) or intermediate (category 2: mangroves, red cliffs or vegetated dunes on one side of the roost).

Microclimate was measured with a portable climate station that recorded substrate temperature (°C), ambient temperature (°C), solar radiation (W/m^2) and wind speed (m/s). Technical specifications are described by Battley et al. (2003). We used the latter three attributes to calculate operative temperatures, that is, the environmental temperatures that knots would experience at a given site (following Wiersma & Piersma 1994, and estimating thermal conductance K_{es} with the generalized equation in Cartar & Morrison 1997). Operative temperatures approached or exceeded body temperature (41 °C; Wiersma & Piersma 1994) during the day (Fig. 2), exposing birds to the risk of heat stress. The temperatures of dry substrates regularly exceeded body temperature but the temperatures of wet substrates did not (Fig. 2). Behavioural evidence suggests that roosting knots use conductive heat loss through the legs to manage heat loads (Battley et al. 2003), a mechanism that can succeed only if the legs are warmer than their environment. We classified daytime climate as 1 (suitably cool) for sites that had a wet substrate, very shallow water or a mixture of both, 3 (too hot) if it was dry and 4 (impossible) if it was too deeply flooded for roosting shorebirds. We used an intermediate category, 2, to describe roost sites where a wet substrate was drying out (surface temperatures in such circumstances were intermediate; Rogers & Taylor 2001) or if the amount of wet ground was limited. Most roost habitats were beaches or exposed mudflats with a wave-washed zone that was wet throughout high tide. Climate classifications for mangrove and salt pan roosts differed from day to day according to tide height and recent rainfall history. At night, in the absence of direct solar radiation, all roosts had a cool microclimate (Fig. 2).

Radiotelemetry and Analysis

Cannon-net catches of knots were made on the northern beaches of Roebuck Bay on 26 and 28 February and 3, 4 and 19 March 2000; catches were made in both the east and west of the bay to increase the likelihood of capturing birds from different feeding areas. Radiotransmitters were attached with superglue to the trimmed back feathers and underlying skin of 25 great knots and 23 red knots; all except two first-year red knots were aged as second-year or older on the basis of moult characteristics (Higgins & Davies 1996). The Holohil BD2 transmitters were small (17 × 8.5 × 5.5 mm) with a whip antenna of 17 cm; at 1.8 g, they were 1.0–1.6% and 0.7–1.3% of the northwestern Australian premigratory masses of red knot and great knot, respectively. Subsequent observations showed that the transmitters were shed in the next prebasic moult (August–October 2000). Each radiomarked bird also received a metal ring and a unique three-ring colour combination. The radiotracked birds departed on northwards

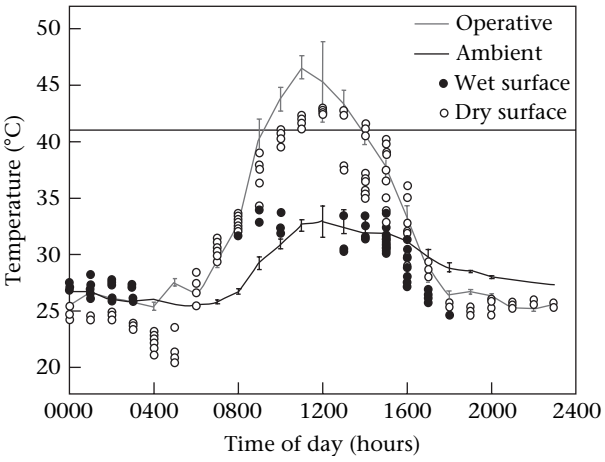

Figure 2. Temperatures of roost sites ($\bar{X} \pm$ SE) in Roebuck Bay during the wet season (data collected February–March and November 2000). The straight line represents body temperature (41 °C, Wiersma & Piersma 1994; personal observation).

migration at the same time as unmarked flockmates (Battley et al. 2004, 2005) and 70% of them (identified by colour rings) have been resighted at the study site in subsequent years, suggesting that there were no adverse long-term effects. The research was approved by the Ethics Sub-Committee for Experimentation on Animals, Griffith University, and was carried out with permits from the Conservation and Land Management Agency, Western Australia.

Radiomarked birds were relocated with 14 continuously operating automatic radiotracking stations positioned on hill tops, dunes or towers (Fig. 1). Stations had omnidirectional antennae and were positioned with little overlap between their detection ranges. This approach prevented us from using triangulation, but increased the area that we could monitor. Technical details on the array are given by Battley et al. (2004). Each transmitter frequency was scanned four times each 20 s; the complete cycle of 52 frequencies (including test frequencies) took 17.3 min. Time and date, frequency, signal strength and strength of background 'noise' were logged on each scan. Experiments with test receivers confirmed that the maximum detection range of these stations was about 0.7–1.0 km. We treated a bird as present at a station if the average signal strength at each 20-s scan was at least 1.4 times that of the average background noise; we checked all such data points against plots of time of day versus date to identify outlying points caused by local interference. The incidence of false signals detected in this way was similar to that of apparent signals received before any radiotransmitters had been deployed, indicating that this data-cleaning procedure was adequate. Automatic radiotelemetry data were supplemented by 174 hand-held radioscans of all frequencies made with portable receivers (TRX 2000S, Wildlife Materials Inc., Carbondale, Illinois, U.S.A.) and directional Yagi antennae; 139 scans were made along the northern shores of Roebuck Bay, and the remainder from more remote sites to seek birds outside the range of the automatic radiotelemetry array. Bearing and strength (weak, medium or strong) of signals were recorded. Detection range of the handheld units was several kilometres, fluctuating with local terrain and the position and behaviour of birds. Finally, 371 resightings of colour-ringed, radiomarked birds were made in the course of telescope scans, usually along the northern beaches.

The time at which rising tide waters first submerged all feeding areas on the intertidal flats corresponded well with the half-way time between low water and high water, and was treated as the end of low tide. We assessed the geographical location of each relocated feeding bird, needed to calculate distance from feeding to roosting areas, for the hour preceding the end of low tide (the end-low feeding period, ELF) and for the mid-low feeding period (MLF, an hour either side of low water). If individuals moved from one feeding area to another during one of these periods, we accepted the location used at the time closest to low water (MLF) or closest to the end of low tide (ELF). Great and red knots typically feed at the sea edge in Roebuck Bay, moving several kilometres from shore as the tide recedes (Rogers 1999). We assumed that, during MLF, birds were feeding at the section of sea edge closest to the automatic radiotracking station that had received their signal, an assumption consistent with daily field observations during the study period. For ELF we assumed that birds were feeding 100 m seaward of the automatic radiotracking station that had received their signal. Errors resulting from these simplifications would have been a few hundred metres at most, small relative to the scale of the distances of several kilometres between feeding and roosting sites.

All roosting records came from one of the nine roosts shown in Fig. 1. The high-tide period when birds were unable to use the intertidal flats lasted 5–6 h. Birds were assigned to a specific roost site only if recorded there within 1 h of high water. Limiting this period prevented confusion of roosts with preroosts, that is, sites where birds sometimes gathered before being forced to move by rising waters. In addition, sites that birds visited briefly and rejected as unsuitable should have been excluded from analysis through use of this restricted high-tide definition. When birds visited more than one site during high tide, the site used closest to high water was treated as the roost.

Signals from automatic tracking station 1 were assigned to CB (Fig. 1), from station 2 to TB, from stations 3, 5, 6, 7, 8 and 9 to NB and from 14 to BP. Station 4 could receive signals from both WF and WOM. On non-neap high tides, all such signals were assigned to WOM, because WF was submerged; on neap high tides, the few signals from station 4 were assigned to WF because this assumption was most consistent with hand-held telemetry data and field observations. Stations 10, 11, 12 and 13 could receive signals from CF, OM and (except station 13) from NB. Signals at these sites were treated as coming from CF on neap tides, because daily field observations or handheld radioscans confirmed that this was the habitat used. On higher tides, signals from these sites were treated as coming from NB if they continued through the high-tide period or from OM if they faded as the tide rose. This fading occurred because birds roosting in OM (open mangroves) walked inland, out of the range of automatic receivers, with the rising tide (Rogers & Taylor 2001). Some records from the inaccessible salt pans (SP) were obtained through handheld telemetry, and we also assigned birds to this habitat if they used OM as a preroost and reappeared at site 13 at the end of high tide, as this was consistent with local field observations (unpublished data). To test whether the incomplete coverage of SP may have skewed our results, we ran models on expanded data sets that assumed that birds of unknown roosting site had roosted at SP and on data sets only including those SP records made with handheld telemetry. These models supported the same conclusions as the data set described above, and they are not presented here.

Modelling

We used two modelling approaches, representing different choice behaviours. Logistic models are commonly used for modelling choice behaviour. We used a form known as the 'conditional logistic model',

appropriate for matched-sample case-control studies and often used in biomedical research and social science studies (Hosmer & Lemeshow 2000; SPSS 2000). In each matched set, the roost chosen was treated as the case and the roosts known not to have been used by that individual on that tide were controls. The descriptor variables on which these sets were matched simultaneously were climate, distance to tall cover, background colour (all ordinal) and distance from feeding area (continuous). The ordinal variables were represented in the conditional logit models as an array of binary variables; the n'th member was set to 1 if the ordinal variable was n, and to 0 if it was not. This enabled nonlinear effects of the ordinal variables to be examined. The model finds the weights (slope coefficients) of the descriptor variables that maximize the conditional likelihood that the observed cases are selected from the matched set. Roost-specific constant terms, a feature of conventional logistic models, are eliminated from the conditional likelihood function, leaving fewer parameters to be estimated. Models were constructed with Systat 10 (SPSS 2000). In effect these models assumed that shorebirds made a probabilistic identification of the most suitable roost, based on a simultaneous assessment of complete information on several environmental factors at each potential roost site.

The other modelling approach, which we called 'bounds-based' or 'bounds', assumed a much simpler choice mechanism in which complete information was not required for all roosts; instead, birds selected the closest roost at which none of climate, tall cover or visibility exceeded critical limits. We calibrated the bounds models by enumerating the 60 possible combinations of the three ordinal descriptor variables, and considering each combination in turn as representing the bounds, finding the closest roost within the bounds. If the roost so found was the same as that selected in practice, the model prediction was taken to be correct. For given subsets of the data, the proportion of roost predictions made correctly was used as a measure of model success. These measures are comparable with the success rate of the conditional logistic models.

The sampling unit in these analyses was the choice made by individual birds on individual tides. Since some individual birds and some choices were sampled many times, we investigated whether pseudoreplication could have influenced our conclusions. We examined four sampling regimes equivalent to: (1) no constraint; (2) one observation taken from each individual; (3) one observation taken from each trial type (i.e. distances to potential roost sites and the climate, tall cover and background colour scores for these roost sites, were the same); (4) one observation taken from each individual on each trial type that it faced. Bootstrap analyses (Manly 1997) of 10 000 random samples from the data sets for each of these sampling regimes were carried out to obtain standard deviations of the proportion of correct roost predictions. There were no significant differences between predictive success of these sampling procedures for any of the logit models (Fisher's omnibus test: $\chi^2_{48} = 31.31$, $P = 0.972$). Predictive success of bounds models varied significantly with sampling regime ($\chi^2_{48} = 86.17$, $P = 0.0006$) but all of these sampling procedures generated success rates consistent with the conclusions drawn in this paper, there was no consistent trend for any particular sampling procedure to have higher predictive success, and the success rate of sampling regime (4) did not differ significantly from the other constrained regimes (paired t tests, using a Dunn–Sidak alpha adjustment of 0.05 as the significance level). Roost choices made by the same individuals on different tides thus appeared to be effectively independent. Except where stated, we present logit and bounds models with individual cases weighted by the inverse of the number of tides on which that individual was exposed to an identical set of options. Models obtained through this weighting procedure (equivalent to sampling regime 4 in the bootstrap analyses) were more conservative (with larger standard errors) than unweighted models.

RESULTS

On neap high tides, 91% of great knots and 83% of red knots roosted at sites that were submerged on non-neap tides, so neaps and non-neaps were modelled separately. Individual birds were typically faithful to small feeding areas during non-neap low tides. On neap low tides, when the area of exposed flats in the western bay was small, some individuals moved to eastern feeding areas, to which they were also site faithful (Fig. 3, Table 2). Log-linear

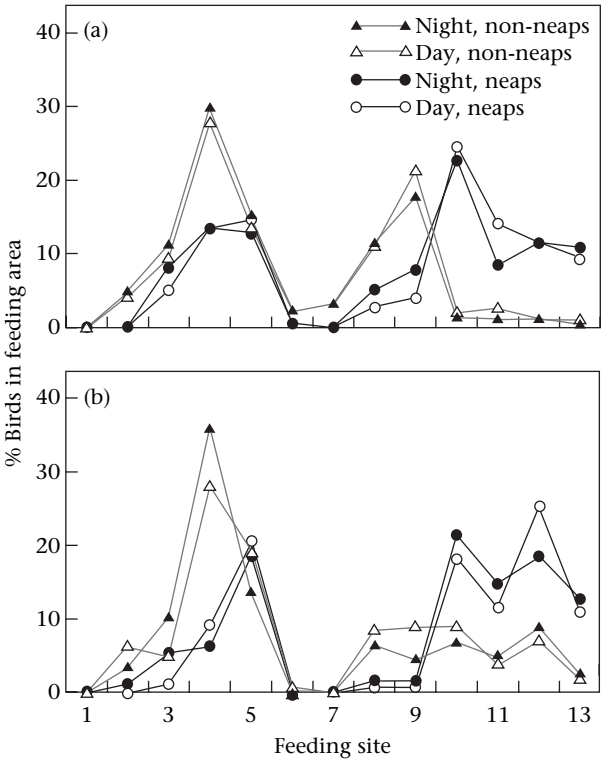

Figure 3. Distribution of radiotracked red and great knots (species combined) (a) in the hour before and after low water and (b) in the last hour of low tide. Numbers along the *X* axis correspond to the nearest automatic tracking station (Fig. 1); data points show the percentage of feeding records per tide type from each site.

Table 2. Fidelity to feeding areas: the percentage of records of individual radiotracked birds that came from either the most frequently used feeding site or the adjacent feeding site (<1 km away)

	Night		Day	
	MLF	ELF	MLF	ELF
Non-neap				
Great knot	91.8 (279)	95.2 (279)	92.9 (338)	91.8 (338)
Red knot	92.3 (376)	88.2 (376)	90.7 (396)	88.4 (396)
Neap				
Great knot	87.9 (64)	96.6 (64)	94.3 (81)	87.3 (81)
Red knot	88.5 (72)	77.5 (72)	80.0 (94)	85.2 (94)

MLF: middle of low tide feeding site; ELF: end of low-tide feeding site; samples sizes are given in parentheses.

models of frequency of use of mid-low feeding sites by day or night, and by tide height, did not differ significantly from models that excluded a day/night term (red knot: $\chi^2_1 = 0.05$, $P = 0.828$; great knot: $\chi^2_1 < 0.01$, $P = 0.995$). In contrast, the high-tide roosts chosen varied markedly according to whether it was day or night (red knot: $\chi^2_1 = 4.79$, $P = 0.029$; great knot: $\chi^2_1 = 4.55$, $P = 0.034$; Fig. 4). Feeding site at low tide cannot therefore be determined solely by the roost site chosen in the subsequent high tide, a condition necessary for the models that follow.

For distance, the logit coefficients (Table 3) describe how much the logit score for a model increases for a unit increase in the independent variables; for the ordinal variables, the coefficients describe how much the logit score increases for a particular value of an independent variable being given (e.g. climate 1) compared to it not being given. The size of the coefficients relative to their standard errors, shown by *t* ratios, indicates the significance of their contribution to the overall model. Different variables contributed to the most effective logit models for neap and non-neap tides, and by day and night (Table 3). Climate

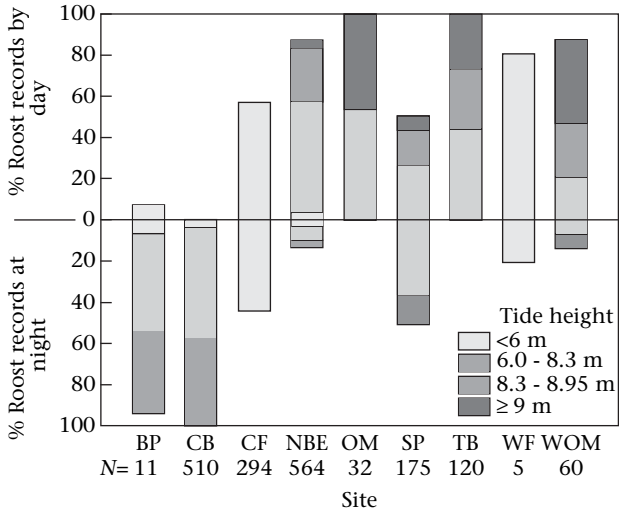

Figure 4. Frequency of use (%) of roost sites (Fig. 1) on tides of different heights 4, by day and at night. *N* = number of roost records.

score had a significant effect only on daytime non-neap high tides; at night, climate score was 1 at all sites and therefore had no effect on the models. In contrast, background colour did not affect models by day but had a significant effect on non-neap high tides at night. The distance from roosts to the nearest tall cover had significant effects in all tide conditions. However, models that included tall cover on night-time non-neap high tides were difficult to interpret. Tall cover and background colour were correlated in these conditions (they were the only models in which there were correlations between predictor variables). Adding tall cover to a model of background colour and distance from feeding grounds to roosts increased the predictive success of night non-neap models, but the tall cover coefficients did not have a monotonic trend. Sites with a tall cover score of 4 were not used, but, beyond that, the effects of tall cover on night-time non-neap high tides did not appear to be linear. In all tide conditions the distance from end-low feeding areas to roosts had a significant effect, with birds preferring nearer roosts.

The independent variables had conceptually similar effects on the bounds models (Table 4). Models that predicted simply that birds flew to the closest roost were correct on 59% (great knot) and 63% (red knot) of daytime non-neap high tides, 30–40% of neap high tides and only 12–16% of night-time non-neaps. On daytime non-neap high tides, constraining climate to a maximum acceptable score (of 1) improved model performance, but it had no effect in other conditions. Constraining background colour to a maximum score (of 1) influenced only non-neap models at night. Constraining proximity of tall cover improved night-time models more than it did daytime models, at least on non-neap tides; on neaps, most birds roosted at one of two sites where there was little variation in distance to tall cover and background colour.

Models that used ELF as the measure of distance from feeding grounds did not differ significantly from those that used MLF (Fisher's omnibus test: bounds models: $\chi^2_{16} = 12.58$, $P = 0.703$; logit models: $\chi^2_{16} = 13.95$, $P = 0.602$; Table 5). However, of movements from an MLF to a nonadjacent ELF during low tide, a disproportionate number took birds closer to their roost sites ($\chi^2_{16} = 146.77$, $P < 0.001$). This effect occurred on daytime non-neaps (great knot: 86.1%, $N = 166$; $\chi^2_1 = 43.373$, $P < 0.001$; red knot: 85.0%, $N = 147$; $\chi^2_1 = 40.985$, $P < 0.001$), on daytime neaps (great knot: 90.3%, $N = 31$; $\chi^2_1 = 10.081$, $P = 0.012$; red knot: 87.5%, $N = 48$; $\chi^2_1 = 13.500$, $P = 0.002$) and on night neaps (great knot: 75.9%, $N = 29$; $\chi^2_1 = 3.879$, $P = 0.330$; red knot: 86.2%, $N = 29$, $\chi^2_1 = 7.603$, $P = 0.046$). On night-time non-neaps there was no such effect (great knot: 57.8%, $N = 147$; $\chi^2_1 = 1.799$, $P = 0.795$; red knot: 59.3%, $N = 150$; $\chi^2_1 = 2.613$, $P = 0.592$), mostly because a movement of birds from feeding sites 3, 4 and 6 towards site 5 occurred more often by day (28.1% of 280 movements) than at night (8.9% of 258 movements). In the chi-square tests above, *P* values given have a Dunn–Sidak adjustment for multiple testing; the same significance results were obtained with weighted data when alpha was adjusted to 0.1 (Quinn & Keough 2002).

Table 3. Conditional logistic regressions with highest predictive success

Model	Variable	Coefficient	*t* ratio	*P*	% Correct
Great knot	Climate 1&2	1.26±0.33	3.864	<0.001	50.6
Day non-neap	Tall cover 1	1.46±0.30	4.926	<0.001	
N=338; 232	Tall cover 2	0.39±0.21	1.863	0.062	
	Distance to ELF	−0.43±0.04	−10.636	<0.001	
Red knot	Climate 1	1.56±0.40	3.893	<0.001	61.1
Day non-neap	Tall cover 1	2.82±0.36	7.838	<0.001	
N=396; 253	Tall cover 2	0.89±0.22	4.037	<0.001	
	Distance to ELF	−0.55±0.05	−11.270	<0.001	
Great knot	Tall cover 1&2*background colour 1	3.76±1.15	3.282	0.001	48.2
Night non-neap	Tall cover 3*background colour 1	6.26±1.27	4.942	<0.001	
N=279; 87	Tall cover 4*background colour 2	−1.62±0.80	−2.036	0.042	
	Background colour 2	3.36±1.32	2.556	<0.011	
	Distance to ELF	−0.114±0.02	−5.376	<0.001	
Red knot	Tall cover 1*background colour 1	1.68±0.56	2.997	0.003	60.7
Night non-neap	Tall cover 2*background colour 1	4.04±0.63	6.380	<0.001	
N=376; 104	Tall cover 3*background colour 1	4.48±0.62	7.290	<0.001	
	Tall cover 3*background colour 2	0.17±0.64	0.272	0.786	
	Distance to ELF	−0.20±0.04	−4.949	<0.001	
Great knot	Tall cover 1	32.00±1.22	26.192	<0.001	85.5
Day neap	Tall cover 2	27.99±0.00			
N=81; 39	Distance to ELF	−0.39±0.19	−2.048	0.041	
Red knot	Tall cover 1	5.98±1.61	3.709	<0.001	76.5
Day neap	Tall cover 2	1.34±0.90	1.486	0.137	
N=94; 54	Distance to ELF	−0.57±0.18	−3.103	0.002	
Great knot	Tall cover 1	31.64±1.05	30.288	<0.001	82.6
Night neap	Tall cover 2	27.21±0.00			
N=64; 43	Distance to ELF	−0.24±0.07	−3.287	0.001	
Red knot	Tall cover 1	3.55±1.05	3.37	<0.001	70.5
Night neap	Tall cover 2	−0.48±0.13	−0.38	0.707	
N=72; 46	Distance to ELF	−0.23±0.06	−3.658	<0.001	

Sample sizes are presented as *N* of matched sets or *N* of cases when weighted. Coefficients of continuous variables and categorical levels of ordinal variables are presented ± SE. The size of the coefficients relative to their SEs is shown by *t* ratios. Variables (microclimate of roost, distance to nearest tall cover, background colour, distance to end of low-tide feeding area, ELF) and interactions between variables were deleted if likelihood ratio tests (SPSS 2000) showed that the restricted and unrestricted models did not differ significantly.

The success rates of bounds and logit models differed significantly (Fisher's omnibus test: $\chi^2_{16} = 40.17$, $P < 0.001$); bounds models had a significantly higher success rate than did the corresponding logit models on day-time non-neap high tides for great knot; in other comparisons, bounds models also had a higher predictive success, but the difference was not statistically significant at $P = 0.05$ after alpha adjustments for multiple hypothesis testing (Table 5).

On non-neap tides, the roost site predicted by bounds models differed from that used on the previous high tide for 68 of 279 great knot movements and 67 of 338 red knot movements by day, and for 76 out of 338 great knot movements and 73 of 396 red knot movements at night. Within such cases, the proportion of birds that roosted on the site used on the previous high tide (27.9% in great knots and 29.9% in red knots by day, 59.2 and 63.0%, respectively, at night), in preference to the site predicted by bounds models (54.4 and 50.2% by day, 17.1 and 34.2% at night), differed significantly in great knots (Fisher's omnibus test: $\chi^2_1 = 22.05$, $P < 0.01$) and red knots ($\chi^2_1 = 22.05$, $P < 0.01$). We extended the bounds-based models with a 'previous-roost correction', using the unweighted data set. We assumed that birds would roost by day at the site that they had used on the previous daytime high tide (if known), and by night at the site used on the previous night-time high tide (if known), unless the site had become completely flooded. This previous-roost correction had significant effects on the predictive success of the models (Fisher's omnibus test: $\chi^2_{16} = 45.06$, $P < 0.001$). It improved prediction rates on non-neap high tides, significantly at night for great knots and at a near-significant level for red knots. On neap high tides, the correction diminished the success rate of model predictions (Table 6).

DISCUSSION

Within specific tide conditions the same categorical levels of the same variables contributed to the most successful roost choice models for great knots and red knots, suggesting that the species use similar roost choice mechanisms. On neap high tides by day and night, roost sites of great knots could be predicted more accurately than those of red knots, but the converse applied on non-neap high tides. We doubt that this reflected any substantial difference in roost

Table 4. Success of predictions of bounds-based models of roost choice (weighted data)

Model	% success with ELF distance only*	Best improvement to distance-only model (percentage points) by constraining†			Final weighted model (% right)	Bounds of final weighted model‡
		Climate	Tall cover	Background		
Day non-neap						
Great knot	59.3	4.2	2.5	0.9	63.5	1, 3, 3
Red knot	63.2	6.8	4.4	3.4	70.0	1, 3, 3
Night non-neap						
Great knot	16.3	0	29.3	43.5	59.9	1, 3, 1
Red knot	12.9	0	29.8	51.7	64.6	1, 3, 1
Day neap						
Great knot	35.0	0	55.6	55.8	90.6	1, 1, 1
Red knot	35.8	0	45.1	45.1	80.9	1, 1, 1
Night neap						
Great knot	39.5	0	52.7	52.7	92.3	1, 1, 1
Red knot	30.1	0	50.0	50.0	80.1	1, 1, 1

*Performance of models that simply assumed that birds flew to the roost closest to the feeding site at the end of low tide (ELF).
†Improvement to this model obtained by adding a single ordinal variable (climate, distance to tall cover or background colour) with a bound to the maximum categorical score possible.
‡The bounds applying to the most successful models. Numbers represent, respectively, climate, tall cover and background colour.

choice mechanisms of the two species, which usually roosted together in mixed flocks. The cause was probably a slight difference in feeding areas. Birds feeding in the west of the bay were near to a different suite of roosts than birds in the east of the bay, and red knots had a slightly more westerly feeding distribution in our samples.

Neap tide models were similar on daytime and night-time high tides, and were affected only by the distance from the feeding areas and the distance from tall cover. In these respects, the structure of neap models differed from those that worked best on non-neaps. However, we doubt that there were genuinely different roost selection mechanisms on neap and non-neap high tides. Most birds spent neap high tides at one of the closest two habitats to their feeding areas: still-exposed intertidal flats in the east of the bay and beaches in the west. As one of these two choices was always acceptable, our models reflect the differences between these two habitats rather than the broader range of roosting habitats surrounding Roebuck Bay. Furthermore, most waders on neap tides roosted on mudflats, the only high-tide habitat used where feeding was possible. Some birds in these situations were seen feeding, although most were loafing; we do not know whether food intake was high enough to

Table 5. Prediction success of models (weighted data) using distance from end of low-tide feeding areas (ELF) and middle of low-tide feeding areas (MLF)

Model	*N*	Logit models (%)			Bounds models (%)			Bounds versus Logit *P**
		ELF	MLF	*P*	ELF	MLF	*P*	
Day non-neap								
Great knot	229	51.8	47.4	0.459	67.0	62.4	0.307	**<0.001**
Red knot	253	61.1	53.1	0.068	70.0	65.8	0.306	0.034
Night non-neap								
Great knot	86	42.6	42.6	0.909	59.9	56.1	0.619	0.018
Red knot	104	58.4	58.3	0.986	64.6	65.7	0.876	0.355
Day neap								
Great knot	39	85.5	83.4	0.802	90.6	90.6	0.999	0.497
Red knot	54	76.5	70.6	0.490	80.9	80.9	1.000	0.583
Night neap								
Great knot	38	80.3	71.4	0.362	92.3	80.6	0.106	0.097
Red knot	45	72.2	65.1	0.466	80.1	68.5	0.173	0.335

P, the probability that paired models did not differ, was calculated with normal deviate *Z* tests (Snedecor & Cochran 1967, page 200).
*Compares the predictive success of ELF bounds and ELF logit models; result in bold was significant after a Dunn–Sidak adjustment of alpha.

Table 6. Prediction success of bounds-based models of roost choice (unweighted data)

Model	Final model without memory (%)	Final model with memory (%)	Gain of memory over nonmemory models: Gain (%)	Gain of memory over nonmemory models: *P*
Day non-neap				
Great knot	61.0	64.2	3.3	0.383
Red knot	69.2	72.0	2.8	0.391
Night non-neap				
Great knot	64.5	76.0	11.5	0.003
Red knot	75.3	80.9	5.6	0.065
Day neap				
Great knot	92.6	82.7	0.1	0.056
Red knot	83.0	76.6	−6.4	0.276
Night neap				
Great knot	93.8	78.1	−15.6	0.011
Red knot	83.3	68.0	−15.3	0.033

P, the probability that memory and nonmemory models did not differ, was calculated with normal deviate *Z* tests (Snedecor & Cochran 1967, page 200).

influence roost choice. We therefore consider the non-neap models more suitable for testing our hypotheses about roost choice.

Roost Choice Criteria Differ by Day and Night

On non-neap high tides, both red and great knots roosted in different places by day and night. Shorebirds have been found using the same roost sites by day and night in some studies (e.g. Warnock & Takekawa 1996; van Gils & Piersma 1999) but often day and night roosts differ (e.g. Hockey 1985; Handel & Gill 1992; Smit & Visser 1993; Rohweder 2001). Shorebirds may have different habitat preferences in daylight and darkness because they are at risk from different predators at night (Sitters et al. 2001). They may also seek particularly safe sites at night so that they can fulfil a physiological need for sleep (Rogers 2003). Our results are consistent with the prediction that avoiding predation risk has a greater influence on roost selection at night. Birds selected roosts that were presumably safer, because these roosts had paler backgrounds and were not close to tall cover, and the birds were prepared to fly longer distances at night (median distance of one-way flights 6–8 km) than by day (median distance of one-way flights 1–3 km; Rogers 2003).

The Risk of Heat Stress Influences Roost Choice

Roost choice was constrained by day, as almost all birds roosted at sites with a wet or moist substrate, where surface temperatures were lower than effective body temperatures. As a result, conductive heat loss through the feet could be used to lower body temperature (Battley et al. 2003). This result did not apply at night; for example at the most commonly used night roost, Cable Beach, many birds roosted on dry sand although wet wave-washed sand was available only a few metres away. In combination with field observations that roosting birds often showed heat avoidance behaviour by day (Battley et al. 2003) but not at night (personal observation), it is reasonable to conclude that roost selection in Roebuck Bay is affected by the need to avoid excessive heat loads. There is mounting evidence that shorebirds may be susceptible to heat stress (Verboven & Piersma 1995; Battley et al. 2003; Rogers et al. 2004). Many migratory shorebirds spend the nonbreeding period in tropical or hot regions, so the need to avoid heat stress may influence roost choice of shorebirds in many parts of the world.

Roosting Shorebirds Are Not Ideal and Free

The distance between feeding areas and roost sites had a significant influence on roost choice models in all tide conditions. It seems therefore that roost choice is not 'free' and that birds try to minimize time investment and travel costs during high tide. This probably minimizes energy expediture on each high tide, although in the absence of direct measurements of energy costs at each roost, we cannot be sure of this.

Conditional logistic models did not predict roost choice as effectively as did bounds-based models. We believe that this is because the bounds-based models were a closer approximation of the decision-making process followed by individual birds. The logit models assumed an ideal distribution of birds, that is, that they had complete knowledge about each potential roost site, and weighed probabilities to decide which roost was most appropriate on a particular tide. The bounds-based models assumed that birds flew to the closest roost at which certain environmental attributes were acceptable, a simpler process that we consider more plausible.

It is unlikely that shorebirds have perfect knowledge about the costs and benefits of every potential roost site before each high tide. By day, shorebirds are presumably able to assess some roost attributes from a distance while airborne, for example whether the site is covered with water, how close they will be forced to roost to tall cover and whether potential predators are nearby. However, these attributes change as the tide rises, so assessments are likely to be imperfect, especially in darkness when sites are harder to see. It would therefore seem advantageous for shorebirds to use experience of roost sites in deciding where to roost, especially at night. The previous-roost corrections that we applied to bounds-based models of roost choice improved model performance on non-neap tides, and, as expected, they improved models more at night. Furthermore, at night the preference for roosts used on the previous high tide was more likely to result in birds using sites that were considered unsuitable according to bounds models, suggesting that when birds had incomplete information, they sometimes roosted at sites that were not optimal. Previous-roost corrections diminished

the performance of bounds-based models on neap high tides. We do not consider this result inconsistent with expectations, as the roost sites most often used on neaps (NB and CF, Fig. 1) were readily visible from the adjacent feeding areas. In such circumstances, memory of the roost used on the previous high tide may be a less appropriate guide to roost choice than what a bird can see of the roosts currently available.

Differences between the performances of models that treated ELF and MLF as the feeding area were not significant. However, in cases when birds did move during low tide, they usually moved to end-low sites that happened to be closer to the roost. The incoming tide submerged these end-low feeding sites (site 5 in the western bay and sites 10–13 in the east) about 20 min (5–10% of a low tide period) later than other mudflats, making it difficult to establish whether the low-tide movements were related to roost choice or foraging decisions. More birds in the west of Roebuck Bay moved towards site 5 (Quarry Beach) by day than at night. By day, Quarry Beach was a frequently used roost, but at night it was seldom used and the majority of western birds flew in the opposite direction to roost on Cable Beach. This result suggests that birds turned down an opportunity to extend their feeding time to avoid moving further from the intended roost.

Even without the use of previous-roost memory corrections, the overall success rate of our bounds-based models was 71.2% by day and 69.5% at night, suggesting that roost choice of shorebirds is predictable. Red and great knots often roost in mixed flocks with other shorebird species, and the factors that influence their roost choice in Roebuck Bay are likely to be important in other sites too, although there is probably regional variation in the tolerance that birds have to some roost attributes. It should therefore be possible (with recalibration) to adapt the models to other species and sites. Bounds models in particular are computationally simple, and could be applied in circumstances where only crude measurements of roost quality are possible. In more applied contexts, foraging models that draw solely on conditions during the feeding period (e.g. Gill et al. 2001; see also van Gils et al. 2004) might be improved by considering the potential constraint of roost availability. Finally, models of roost choice could be valuable tools in the management of shorebird sites. They can be used to develop profiles of the factors that make a site suitable for roosting shorebirds, and to predict whether specific roosts will continue to be used if habitat changes occur.

Our study indicates that the study of roost choice can provide important insights into the adaptive basis for daily strategies, with the prospect of insights into the cognitive architecture of the birds under study (Dukas 1998; Shettleworth 1998; Hauser 2001). For example, the predictive success of bounds models exceeded that of logistic models, suggesting that shorebirds make decisions based on thresholds rather than on probability algorithms that are much more information and computationally demanding. The comparison of models also suggested the importance of memory in situations when visual information on actual roost site conditions was hard to obtain (i.e. at night). Finally, the comparisons between logical, environment-fed models and actual behaviours informed us about the environmental features that shorebirds valued in tropical northwest Australia: (1) proximity of roosting and feeding sites, probably to conserve energy expediture, (2) wet roosting sites during daytime to avoid overheating, and (3) open roosts bounded by pale substrates, probably to enhance the ability to detect approaching predators. By our criteria the roosts chosen at night were safer than those used by day, but they were more distant, indicative of the price that shorebirds are prepared to pay for their safety (cf. Brown 1988; van Gils et al. 2004).

Acknowledgments

Funding essential to our research was provided by the National Geographic Society (Washington, D.C.), George Alexander Fund (Melbourne, Australia), Ian Potter Foundation (Melbourne, Australia), Stuart Leslie Bird Research Award (Birds Australia), Australian Bird Environment Foundation, a PIONIER grant to T.P. from the Netherlands Organisation for Scientific Research (NWO), Griffith University and a postgraduate scholarship to D.I.R. from Charles Sturt University. Adrian Boyle, Andrew Dunn, Chris Hassell, Janet Sparrow and Jonny Schoenjahn played important parts in initial exploration for the key roost sites of Roebuck Bay. For their assistance during the radiotelemetry expedition we thank Broome Bird Observatory staff (Bill Rutherford, Adrian Boyle, André and Rosalind Joubert), Joe Crisafio Proton, Autotrans, Pacific Transport, Ardrossan Customs Service, and the Western Australian Department of Conservation and Land Management (CALM), especially Alan Grosse (Broome), Belinda Dettmann (ABBBS), and Dick and Barbara Cooper (ABSA mist-net service). Chris Hassell and Adrian Boyle led the cannon-netting. Petra de Goeij, Jan van de Kam, Anne Dekinga, Betty Gilbert, Anita Koolhaas, Grant Pearson, Mavis Russell, Humphrey Sitters and Bernard Spaans gave essential fieldwork assistance. Iain Taylor, Lance Workman and two anonymous referees provided valuable comments on the manuscript; Dick Visser prepared the figures.

References

Battley, P. F., Piersma, T., Dietz, M. W., Tang, S., Dekinga, A. & Hulsman, K. 2000. Empirical evidence for differential organ reduction during trans-oceanic bird flight. *Proceedings of the Royal Society of London, Series B*, **267**, 191–195.

Battley, P. F., Rogers, D. I., Piersma, T. & Koolhaas, A. 2003. Behavioural evidence for heat-load problems in great knots in tropical Australia fuelling for long-distance flight. *Emu*, **103**, 97–103.

Battley, P. F., Piersma, T., Rogers, D. I., Dekinga, A., Spaans, B. & van Gils, J. A. 2004. Do body condition and plumage during fuelling predict northwards departure dates of great knots *Calidris tenuirostris* from North-west Australia? *Ibis*, **146**, 46–80.

Battley, P. F., Rogers, D. I., van Gils, J. A., Piersma, T., Hassell, C. J., Boyle, A. & Yang, H.-Y. 2005. How do red knots *Calidris*

canutus leave Northwest Australia in May and reach the breeding grounds in June? Predictions of stopover times, fuelling rates and prey quality in the Yellow Sea. *Journal of Avian Biology*, **36**, 494–500.

Brown, J. S. 1988. Patch use as an indication of habitat preferences, predation risk and competition. *Behavioral Ecology and Sociobiology*, **22**, 37–48.

Burton, N. H. K., Evans, P. R. & Robinson, M. A. 1996. Effects on shorebirds of disturbance, the loss of a roost site and its replacement by an artificial island at Hartlepool, Cleveland. *Biological Conservation*, **77**, 193–201.

Cartar, R. V. & Morrison, R. I. G. 1997. Estimating metabolic costs for homeotherms from weather data and morphology: an example using calidrine sandpipers. *Canadian Journal of Zoology*, **75**, 94–101.

Collins, P., Boyle, A., Minton, C. D. T. & Jessop, R. 2001. The importance of inland claypans for waders in Roebuck Bay, North-western Australia. *Stilt*, **38**, 4–8.

Cresswell, W. 1994. Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *Journal of Animal Ecology*, **63**, 589–600.

Daan, S. 1981. Adaptive daily strategies in behaviour. In: *Handbook of Behavioral Neurobiology.Vol. 4: Biological Rhythms* (Ed. by J. Aschoff), pp. 275–298. New York: Plenum.

Davidson, N. C. & Rothwell P. (Eds) 1993. Disturbance to waterfowl on estuaries. Special issue of the *Wader Study Group Bulletin*, **68**, 1–106.

Dukas, R. (Ed.) 1998. *Cognitive Ecology: the Evolutionary Ecology of Information Processing and Decision Making* Chicago: University of Chicago Press.

Gill, J. A., Sutherland, W. J. & Norris, K. 2001. Depletion models can predict shorebird distribution at different spatial scales. *Proceedings of the Royal Society of London, Series B*, **268**, 369–376.

van Gils, J. & Piersma, T. 1999. Day- and nighttime movements of radiomarked knots, *Calidris canutus*, staging in the western Wadden Sea in July–August 1995. *Wader Study Group Bulletin*, **89**, 36–44.

van Gils, J. A., Edelaar, P., Escudero, G. B. & Piersma, T. 2004. Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology. *Oikos*, **104**, 197–204.

Handel, C. M. & Gill, R. E. 1992. Roosting behaviour of pre-migratory dunlins (*Calidris alpina*). *Auk*, **109**, 57–72.

Hauser, M. 2001. *Wild Minds. What Animals Really Think*. London: Penguin.

Higgins, P. J. & Davies, S. J. J. F. (Eds) 1996. *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 3: Snipe to Pigeons.* Melbourne: Oxford University Press.

Hockey, P. A. R. 1985. Observations on the communal roosting of African black oystercatchers. *Ostrich*, **56**, 52–57.

Hosmer, D. W. & Lemeshow, S. 2000. *Applied Logistic Regression*. New York: J. Wiley.

Lindström, Å. 1991. Maximum fat deposition rates in migrating birds. *Ornis Scandinavica*, **22**, 12–19.

Luís, A., Goss-Custard, J. D. & Moreira, M. H. 2001. A method for assessing the quality of roosts used by waders during high tide. *Wader Study Group Bulletin*, **96**, 71–74.

Manly, B. F. J. 1997. *Randomisation, Bootstrap and Monte Carlo Methods in Biology*. 2nd edn. London: Chapman & Hall.

Mitchell, J. R., Moser, M. E. & Kirby, J. S. 1988. Declines in midwinter counts of waders roosting on the Dee Estuary. *Bird Study*, **35**, 191–198.

Myers, J. P. 1984. Spacing behavior of nonbreeding shorebirds. In: *Shorebirds: Migration and Foraging Behavior* (Ed. by J. Burger & B. L. Olla), pp. 271–321. New York: Plenum.

Pepping, M., Piersma, T., Pearson, G. & Lavaleye, M. (Eds) 1999. *Intertidal Sediments and Benthic Animals of Roebuck Bay, Western Australia. NIOZ Report 1999–3*. Texel: Netherlands Institute for Sea Research (NIOZ).

Piersma, T. & Baker, A. J. 2000. Life history characteristics and the conservation of migratory shorebirds. In: *Behaviour and Conservation* (Ed. by L. M. Gosling & W. J. Sutherland), pp. 105–124. Cambridge: Cambridge University Press.

Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P. & Wiersma, P. 1993. Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. *Netherlands Journal of Sea Research*, **31**, 331–357.

Piersma, T., Verkuil, Y. & Tulp, I. 1994. Resources for long-distance migration of knots *Calidris canutus islandica* and *C. c. canutus*: how broad is the temporal exploitation window of benthic prey in the western and eastern Wadden Sea? *Oikos*, **71**, 393–407.

Piersma, T., Bruinzeel, L., Drent, R., Kersten, M., van der Meer, J. & Wiersma, P. 1996. Variability in basal metabolic rate of a long-distance migrant shorebird (red knot, *Calidris canutus*) reflects shifts in organ sizes. *Physiological Zoology*, **69**, 191–217.

Piersma, T., Rogers, D. I., Gonzalez, P., Zwarts, L., Niles, L. J., de Lima Serrano do Nascimento, I., Minton, C. D. T. & Baker, A. J. 2005. Fuel storage rates in red knots worldwide: facing the severest ecological constraint in tropical intertidal conditions? In: *Birds of Two Worlds: the Ecology and Evolution of Migratory Birds* (Ed. by R. Greenberg & P. P. Marra), pp. 262–274. Baltimore: Johns Hopkins University Press.

Quinn, G. P. & Keough, M. J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.

Rehfisch, M. M., Clark, N. A., Langston, R. H. W. & Greenwood, J. D. 1996. A guide to the provision of refuges for waders: an analysis of 30 years of ringing data from the Wash, England. *Journal of Applied Ecology*, **33**, 673–687.

Rehfisch, M. M., Insley, H. & Swann, B. 2003. Fidelity of overwintering shorebirds to roosts on the Moray Basin, Scotland: implications for predicting impacts of habitat loss. *Ardea*, **91**, 53–70.

Rogers, D. I. 1999. What determines shorebird feeding distribution in Roebuck Bay? In: *Intertidal Sediments and Benthic animals of Roebuck Bay, Western Australia. NIOZ report 1999–3* (Ed. by M. Pepping, T. Piersma, G. Pearson & M. Lavaleye), pp. 145–174. Texel: Netherlands Institute for Sea Research (NIOZ).

Rogers, D. I. 2003. High-tide roost choice by coastal waders. *Wader Study Group Bulletin*, **100**, 73–79.

Rogers, D. I. & Taylor, I. 2001. *Conservation and Ecology of Migratory Shorebirds in Roebuck Bay, North-western Australia. Final Report for the Wetlands Unit, Environment Australia*. Albury: Charles Sturt University.

Rogers, D. I., Boyle, A. & Hassell, C. 2001. Occasional wader counts No. 5: wader counts on Kidneybean Claypan and adjacent Roebuck Plains, North-western Australia. *Stilt*, **38**, 57–63.

Rogers, D. I., Piersma, T., Lavaleye, M., Pearson, G. B., de Goeij, P. & van de Kam, J. 2003. *Life Along Land's Edge. Wildlife on the Shores of Roebuck Bay, Broome*. Kensington: Western Australian Department of Conservation and Land Management.

Rogers, D. I., Battley, P. F., Sparrow, J., Koolhaas, A. & Hassell, C. J. 2004. Treatment of capture myopathy in shorebirds: a successful trial in North-western Australia. *Journal of Field Ornithology*, **75**, 157–164.

Rohweder, D. A. 2001. Nocturnal roost use by migratory waders in the Richmond River Estuary, Northern New South Wales, Australia. *Stilt*, **40**, 23–28.

Shettleworth, S. J. 1998. *Cognition, Evolution, and Behavior*. New York: Oxford University Press.

Sitters, H. P., Gonzalez, P. M., Piersma, T., Baker, A. J. & Price, D. J. 2001. Day and night feeding habitat of red knot in Patagonia: profitability versus safety? *Journal of Field Ornithology*, **72**, 86–95.

Smit, C. & Visser, G. M. 1993. Effects of disturbance on shorebirds: a summary of existing knowledge from the Dutch Wadden Sea and Delta area. *Wader Study Group Bulletin*, **68** (Supplement), 6–19.

Snedecor, G. W. & Cochran, W. G. 1967. *Statistical Methods*. 6th edn. Ames: Iowa State University Press.

SPSS Inc. 2000. *Systat 10.0*. Chicago: SPSS Inc.

Tieleman, B. I. & Williams, J. B. 1999. The role of hyperthermia in the water economy of desert birds. *Physiological and Biochemical Zoology*, **72**, 87–100.

Verboven, N. & Piersma, T. 1995. Is the evaporative water loss of knots *Calidris canutus* higher in tropical than in temperate climates? *Ibis*, **137**, 308–316.

Warnock, S. E. & Takekawa, J. Y. 1996. Wintering site fidelity and movement patterns of western sandpipers *Calidris mauri* in the San Francisco Bay estuary. *Ibis*, **138**, 160–167.

Whitfield, D. P. 2003. Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk *Accipiter nisus* predation. *Journal of Avian Biology*, **34**, 163–169.

Wiersma, P. & Piersma, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of knots. *Condor*, **96**, 257–279.